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Multiyear drought-induced morbidity preceding tree death in southeastern U.S. forests

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Abstract. Recent forest diebacks, combined with threats of future drought, focus attention on the extent to which tree death is caused by catastrophic events as opposed to chronic declines in health that accumulate over years. While recent attention has focused on large-scale diebacks, there is concern that increasing drought stress and chronic morbidity may have pervasive impacts on forest composition in many regions. Here we use long-term, whole-stand inventory data from southeastern U.S. forests to show that trees exposed to drought experience multiyear declines in growth prior to mortality. Following a severe, multiyear drought, 72% of trees that did not recover their pre-drought growth rates died within 10 yr. This pattern was mediated by local moisture availability. As an index of morbidity prior to death, we calculated the difference in cumulative growth after drought relative to surviving conspecifics. The strength of drought-induced morbidity varied among species and was correlated with drought tolerance. These findings support the ability of trees to avoid death during drought events but indicate shifts that could occur over decades. Tree mortality following drought is predictable in these ecosystems based on growth declines, highlighting an opportunity to address multiyear drought-induced morbidity in models, experiments, and management decisions.

Key words: adaptive management; drought; forest; long-term data; morbidity; mortality; Piedmont Plateau, North Carolina, USA; southern Appalachian Mountains, North Carolina, USA; tree

Introduction

The risk of tree mortality from drought stress threatens forest structure and function at multiple time scales (Dietze and Moorcroft 2011, Choat et al. 2012, Anderegg et al. 2013b), with potentially important ecological and economic consequences. The expectation of increasing frequency and severity of drought events in the future (Li et al. 2011, Dai 2012) may require novel forest policy and management practices (Millar et al. 2007, Puettmann 2011). However, attributing tree mortality to discrete drought events can be difficult because tree mortality rates are typically low and many of the long-term data sets used to analyze drought effects have intervals of multiple years between measurements (Klos et al. 2009, Metcalf et al. 2009). These challenges create uncertainties in efforts to predict and model

drought-induced tree mortality (McDowell et al. 2011). This study provides information on the time scale of tree decline following severe drought across sites and species.

Tree mortality trends during and after drought can be obscured by the multiple, interacting factors that contribute to declining health (Franklin et al. 1987), termed morbidity. For example, trees that die during drought are often susceptible before the drought occurs (Ogle et al. 2000, Macalady and Bugmann 2014). Species are expected to differ in their vulnerability and exposure to stress within a site, which can create variation among individuals in mortality risk (Clark et al. 2010). Trees also have multiple ways to avoid stress during drought (e.g., resistance to cavitation, stomatal control, and xylem refilling; Meinzer et al. 2010, McDowell et al. 2011), although these mechanisms can progressively degrade over time and multiple drought events (Anderegg et al. 2013b). Additionally, drought events could incite morbidity and increase future mortality risk for surviving trees (Pedersen

1998). The extent to which morbidity induced by and following drought could contribute to mortality across species and environments has not been quantified. If extensive, drought-induced morbidity may signal risks for forests beyond well-publicized die-off events (Franklin et al. 1987, Archaux and Walters 2006).

Here, we assess tree decline following drought with whole-stand data of annual tree records from forests in two regions of the southeastern United States, including >28 000 trees from 35 species over 20 yr (1993–2012). We tracked individual trees for up to a decade after a severe, prolonged drought in 2000–2002 across two distinct climatic zones, the Piedmont Plateau (mean annual temperature [MAT] = 15.5°C, mean annual precipitation [MAP] = 1140 mm) and the southern Appalachian Mountains (MAT = 12.6°C, MAP = 1805 mm). We test the hypothesis that mortality can follow a progressive, drought-induced decline in growth by examining the effects of post-drought recovery and local moisture availability on decadal tree survival after this drought. We consider the factors that contributed to recovery for the trees that survived. Then we use these responses to develop a new index that quantifies trends in morbidity leading up to death across species, based on the difference in cumulative growth between comparable individuals that survived and died.

METHODS

Observations of individual trees come from long-term demographic monitoring plots in the southern Appalachian Mountains (Coweeta Hydrologic Laboratory, Macon County) and the Piedmont Plateau (Duke Forest, Orange County) of North Carolina, USA. Data on individual tree growth (Clark et al. 2007) and survival (Wyckoff and Clark 2002, Metcalf et al. 2009) were collected from each plot over a period of 8–21 yr. Each tree has a unique observation history, and data models are fit to observations to trace each individual's growth and survival probability annually. From 28 879 measured trees, 5818 died during the study. Further details on field methods, models, and diagnostics can be found in Clark et al. (2010). Each individual was exposed to the site-level environmental conditions as well as local environmental variation. We used the topographic wetness index (ω), calculated with local elevation data, as an indicator of tree moisture availability. The topographic wetness index describes local drainage patterns in a catchment and provides a relative measure of soil moisture availability in these forests (Moore et al. 1993, Hwang et al. 2009; A. B. Berdanier and J. S. Clark, *unpublished data*). We also considered the influence of local basal area, calculated as the summed basal area of neighbors within 10 m of each tree,

and the change in local basal area over the study period.

Individual growth rates were quantified with estimates of annual diameter increment (cm/yr). For relative growth vigor preceding mortality (γ), we identified all individuals that died during the study and, for each individual that died (i), we selected conspecific trees (same species, same plot) that survived for the entire study (j) and calculated the mean growth rate in each year (g_t). Then, we took the log ratio of the growth rate for each dead tree ($g_{t,i}$) vs. the growth rate of the average conspecific in each year prior to their death, $\gamma_{t,i} = \ln(g_{t,i} / \overline{g_{t,j}})$ Negative vigor values indicate growth rates that are lower in dead trees than in surviving trees.

For comparisons of individual growth before and after drought (ρ, an indicator of recovery or morbidity), we averaged the post-drought growth rates across surviving years (for trees that died) or the remainder of the study (for trees that survived) for each individual to estimate growth after drought ($\overline{g_{\text{post},i}}$). Then, we calculated the mean pre-drought growth rate for each individual ($\overline{g_{\text{pre},i}}$) and used the log ratio of mean growth rates after and before the drought as an index of recovery $\rho_i = \ln(\overline{g_{\text{post},i}} / \overline{g_{\text{pre},i}})$. Here, negative values indicate lower growth after the drought than before the drought. We assumed recovery if post-drought growth rate ratios were greater than the 10th percentile of surviving trees. We tested the effects of individual growth recovery (ρ_i) and individual wetness conditions (ω_i) on decadal survival (s_i) following the 2000–2002 drought with a Bayesian logistic regression

$$s_i \sim \text{Bernoulli}(\pi_i)$$

$$\text{logit}(\pi_i) = \beta_0 + \beta_1 \rho_i + \beta_2 \omega_i + \beta_3 \rho_i \omega_i.$$

where ϖ_i is the probability of survival and βs are statistical effect parameters. Parameters were fit across species and sites that were exposed to and survived the 2000–2002 drought (n = 11 662 observations). For surviving trees, we examined the effect of tree size (natural log of individual diameter) and the change in local basal area (natural log of basal area loss within 10 m) on individual growth recovery with a Bayesian linear regression. We used uninformative normal priors on all regression parameters and ran 50 000 Markov chain Monte Carlo (MCMC) iterations with the MCMCpack package (Martin et al. 2011) in R (R Core Team 2015) to generate posterior estimates of each parameter.

To calculate cumulative morbidity for each individual that died (χ_i), we first summed the growth between the drought and eventual mortality (d_i), $G_i = \sum_{t=2003}^{d_i} g_{i,t}$ Next, we summed the growth for each surviving conspecific (j,i) over the same time period and took the mean across survivors, $G_{j,i} = \sum_{t=2003}^{d_i} g_{j,t}$. Then, we calculated the log ratio of cumulative
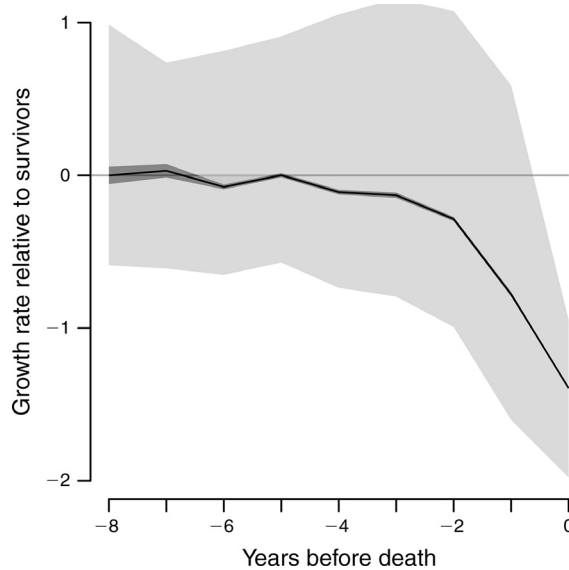
FIG. 1. Decline in growth vigor prior to death (γ). Growth rates of trees that died were lower than mean rates of surviving comparable trees for multiple years prior to death (line and dark gray shading shows mean ± SE) although there was large variation across individuals (light gray shading shows 95% range of observations).

growth for the mean conspecific over the time period vs. that of each dead tree, $\chi_i = \ln(G_{j,i}/G_i)$. We generated summary statistics for each species that had at least 10 dead individuals with these individual measures and compared these values to a species drought-tolerance index that incorporated information on physiological responses to water stress and habitat occurrence observations (Niinemets and Valladares 2006).

RESULTS

Three severe drought events occurred during the 20-yr study, including a prolonged drought in 2000–2002 that was preceded by a decade of mesic (on average) conditions. During this drought, the June-July-August Palmer Drought Severity Index (JJA PDSI) in the Appalachian Mountains exceeded the 90th percentile of 100-yr drought severity and the 2002 JJA PDSI in the Piedmont Plateau was in the 96th percentile. Survival rates remained high across these events and showed no relationship with drought severity between censuses (Appendix A: Table A1). In contrast, we found decreased growth during drought years across sites and species (Appendix A: Table A2). For the trees that died during drought years ($n = 823$, 14% of total deaths), 87% had pre-drought growth rates that were below the mean for conspecific individuals in the same stands over periods of 2–5 yr. Declining growth rates suggest that these trees were susceptible for multiple years before the drought, consistent with tree-ring

observations during drought events in other ecosystems (e.g., Macalady and Bugmann 2014). For the remaining trees that survived the drought, we examined whether drought exposure further affected their long-term growth and survival.

We compared the health statuses of trees that survived and died after droughts to account for pre-drought risk. Tree mortality can follow declines in radial stem growth over multiple years (Waring 1987, Wyckoff and Clark 2002), which we observed as a decline in vigor compared to conspecific trees (Fig. 1). We examined if the growth rates of trees changed following drought and, if so, whether it was associated with a decline in survival. We found that decadal survival for trees that were exposed to the 2000–2002 drought was positively related to both post-drought recovery ($\beta_1 = 5.64$, 95% credible interval [CI] = 5.26–6.05) and tree moisture availability ($\beta_2 = 0.14$, 95% CI = 0.08–0.19), a relationship that was consistent across sites and species. Decadal survival was independent of local basal area before the drought, consistent with findings in other studies (Floyd et al. 2009, Klos et al. 2009, Ganey and Vojta 2011).

Trees that survived the drought but died within the next 10 yr had lower growth rates on average for the rest of their lives than they did prior to drought (54% and 71% of pre-drought levels in the Piedmont Plateau and Appalachian Mountains; Fig. 2). This pattern held regardless of the post-drought time interval examined, although it was exacerbated following exposure to additional droughts (Appendix A: Fig. A1). Similar to the trees that died during drought and consistent with our observation
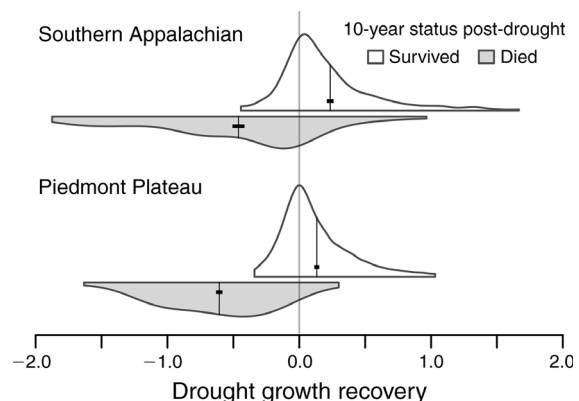

FIG. 2. Post-drought survival depends on growth recovery (ρ). Growth rates for trees that died in the decade after drought (shaded) were lower than pre-drought levels in both the Appalachian Mountains (top) and the Piedmont Plateau (bottom); rates are shown as relative density of observations. Trees that survived throughout the study (not shaded) showed increased growth in years following drought, on average. Vertical lines and horizontal bars show mean ± SE and distribution intervals range over 95% of individuals.

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of multiyear declines prior to death (Fig. 1), 64% of the trees that died in the next 10 yr had pre-drought growth rates that were lower than the mean surviving conspecific. Those trees were performing poorly compared to their neighbors prior to the drought and experienced further growth declines after the drought. Trees that survived for over 10 yr following the drought resumed pre-drought growth patterns and had higher growth rates than before the drought on average while trees that ultimately died showed continued morbidity. For the trees that survived, their growth recovery was positively related to both tree size (posterior mean effect = 0.129, 95% CI = 0.121–0.137) and, less strongly, the loss of neighbor basal area over the study period (posterior mean effect = 0.016, 95% CI = 0.007–0.024). Of all trees

that did not recover pre-drought growth rates, 72% died within 10 yr.

Survival was higher for trees in wet local environments than those in dry areas, in agreement with another study in this region (Klos et al. 2009). The negative effect of declining growth on survival was amplified in dry locations, based on the positive interaction between drought recovery and tree moisture availability from the topographic wetness index (β_3 = 0.38, 95% CI = 0.20–0.56). In contrast, survival in the relatively mesic period preceding this drought (1993–1999) responded similarly to growth declines but showed no association with the topographic wetness index (Appendix A: Table A3). While the multiyear declines in growth preceding mortality are similar between the two distinct time periods, these declines
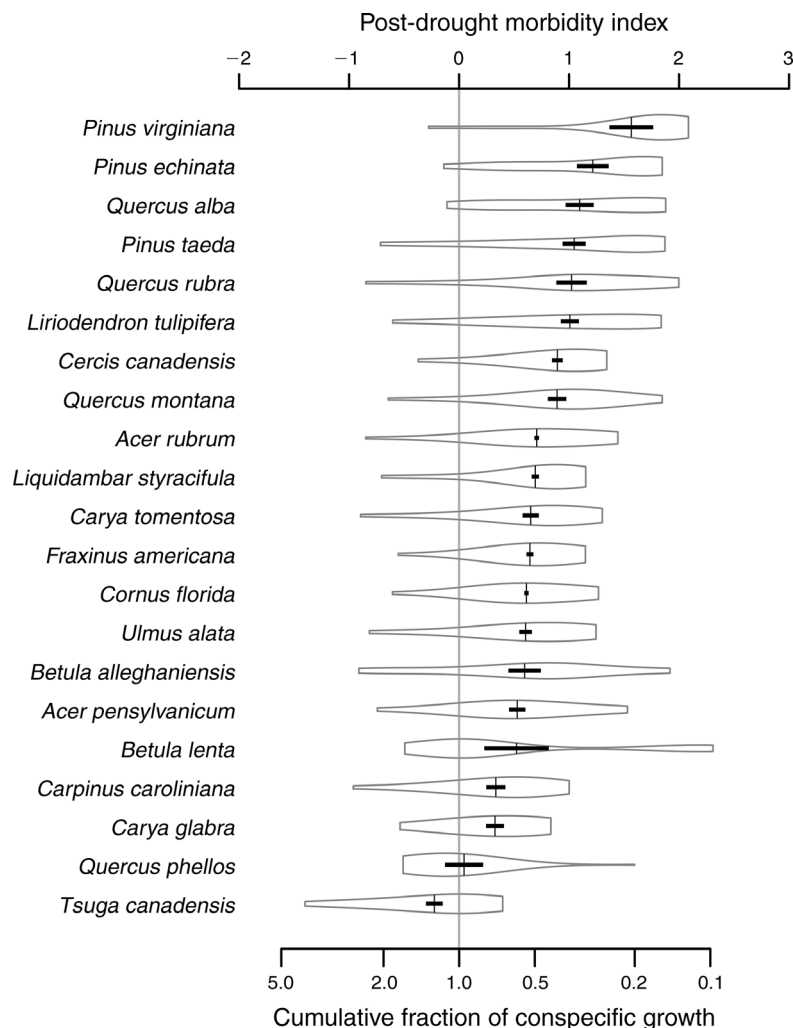

FIG. 3. Drought-induced morbidity preceding tree death (χ). Post-drought growth morbidity prior to death varied among species, with trees of many species showing cumulative depressions in growth (positive morbidity values) compared to surviving conspecifics prior to mortality. Vertical lines and horizontal bars show mean ± SE and distribution intervals range over 95% of individuals.

were greatest for trees in dry local environments only after the drought.

Our morbidity measure quantifies the cumulative differences in growth between trees that die and comparable survivors and provides an index for the risk of mortality from growth stress following drought. The cumulative morbidity for trees that were exposed to the 2000–2002 drought and ultimately died varied by species (Fig. 3), with most species showing a pattern of decline that extended for multiple years. Averaged across species, mortality risk increased when the cumulative diameter growth fell below 54% of the growth of surviving conspecifics (range across species = 21–125%), consistent with our observation that mortality is a multiyear process (Fig. 1). The only species that experienced mortality at growth rates above surviving conspecifics on average (negative morbidity) was *Tsuga canadensis*, which is currently experiencing rapid declines from an exotic insect that equally targets healthy trees (Nuckolls et al. 2009). The mean species morbidity index values were correlated with a species drought-tolerance index ($r = 0.713$, Fig. 4; Niinemets and Valladares 2006), where species characterized as drought intolerant were relatively unable to withstand large cumulative depressions in growth prior to mortality.

DISCUSSION

Our results demonstrate a pattern of multiyear declines in tree growth following a severe drought across sites in the southeastern United States. These declines were related to a reduced survival probability over the following decade and associated with local drought severity. While most of the trees that were unable to recover from this stress ultimately died, the cumulative morbidity that trees experienced prior to death varied among species (Fig. 3), indicating possible shifts in species composition under different climate scenarios. Dying trees that have high morbidity prior to death are under stress relative to surviving conspecifics and are prone to die in the years after drought because of their inability to recover (Fig. 2), especially if they experience subsequent droughts. The finding that drought can set in motion protracted morbidity leading to eventual death suggests that drought frequency and severity may already be changing forest composition and structure beyond regions where large diebacks are observed (Allen et al. 2010). For most species here, drought stress contributes to deteriorating health over multiple years, exacerbated by dry habitats.

Our observation that mortality can be prolonged following drought events could result from interactions between hydraulic status, carbon balance, and additional contributing factors that lead to growth morbidity and predispose an individual to die (Pedersen 1998,
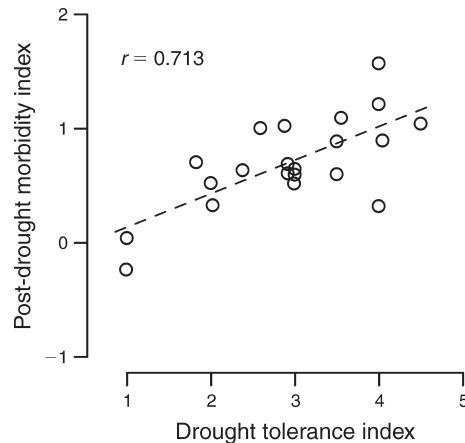

FIG. 4. Positive correlation between the mean posterior post-drought morbidity index and species drought tolerance index. Dashed line shows a linear regression between indices.

McDowell et al. 2011). For example, while trees may avoid systemic hydraulic failure over short time periods (Fisher et al. 2006, Plaut et al. 2012), nonlethal loss of canopy conductance could be a precursor for multiyear morbidity (Anderegg et al. 2013*b*). Moreover, many of the trees that died during and after drought had lower vigor prior to the drought than surviving conspecifics, indicating potential predisposition to drought vulnerability, possibly from interactions with pathogens, insects, or habitat (Franklin et al. 1987, Anderegg et al. 2015).

The long-term nature of tree decline following drought in southeastern U.S. forests has important implications for the monitoring and management of drought impacts in these ecosystems (Anderegg et al. 2013*a*). The relationship between the ability to endure cumulative morbidity prior to death and species drought tolerance (Fig. 4) highlights differing degrees of vulnerability among species. Our cumulative morbidity measure, combined with the relationship between growth and mortality, may provide accurate predictions for forest responses to droughts of varying frequency and intensity in dynamic global vegetation models, which already have strong growth modules (McDowell et al. 2011). Field monitoring and adaptive management efforts can focus on growth morbidity as a predictor of drought mortality with particular attention to drought-intolerant species, which may die relatively suddenly, and trees that show growth depressions after drought, which may be more likely to die in the following years.

The importance of growth recovery after drought for long-term survival raises questions about why the survivors were able to recover. We found that growth recovery among survivors was higher for larger trees and for trees that lost more of their neighboring basal area. We hypothesize that both of these responses could

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be influenced by individual access to soil moisture. Large individuals may have access to deep soil layers that are inaccessible to smaller neighbors (Donovan and Ehleringer 1991) and the loss of neighboring trees may alleviate stress by increasing local light and moisture availability (Aussenac and Granier 1988, Bréda et al. 1995, Elkin et al. 2015). This pattern supports the multiyear advantages of thinning as a tool to reduce mortality risk by reducing post-drought morbidity (D'Amato et al. 2013). Thinning that promotes growth recovery may forestall mortality for at-risk trees. Future studies can explicitly test these hypotheses and assess the influence of physiological status on growth morbidity across species and environments.

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Supporting Information

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